Application of vertebrate trace fossils to palaeoenvironmental analysis

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ABSTRACT

This is a review of the main uses of vertebrate trace fossils, ichnofabrics and ichnofacies in the palaeoenvironmental analysis of sedimentary sequences. The article accounts for the significant developments produced in the last three decades, including the application of the ichnofacies concept to vertebrate trace fossils. Recognition of footprints in cross-sectional view and their distinction from inorganic structures and burrow fills, is first discussed. The response of different substrates, showing contrasting water content and imprinted by different animals or devices, is compared in terms of the morphology of the resultant footprint. Trackways with sand crescents are typical of aeolian cross-strata and are absent in associated flat-lying to low-angle deposits. Thick packages of highly bioturbated sandy dune and interdune sediments have been interpreted as reflecting periods of increased rainfall. Neoichnological observations in modern lake basins suggest that distinct zones can be recognized in the margins of fossil ponds and lakes, including onshore, shoreline and shallow subaqueous zones. Abundant flamingo-like footprints and flamingo nest mounds are good indicators of alkaline and/or saline lake waters. Hippopotamus trails are found closely associated with modern and fossil freshwater wetlands. Dinosaur and pterosaur swim traces from lacustrine and fluvial deposits can be used to estimate water depth. Turtle, crocodile, amphibian, hippopotamus and fish swim traces allow one to infer a subaqueous substrate. Certain modern intertidal fish feeding traces are oriented with the predominant tidal current and can be used as palaeocurrent indicators. The preferential orientation of tetrapod trackways in lacustrine and fluvial deposits is analyzed. Vertebrate trace fossils can help to infer discharge variability in fluvial channels. The descriptions of vertebrate ichnofabrics are commonly limited to heavily bioturbated beds due to trampling by vertebrates, and to a few examples of ichnofabrics with discrete trace fossils. The nature and implications of the recognized vertebrate ichnofacies are still being debated and have a limited utility in palaeoenvironmental analysis. The distinction of a potential vertebrate burrow ichnofacies in carbonate-bearing palaeosols is proposed to represent well-drained soils, developed under arid or semiarid climate.

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1. Introduction

Vertebrate trace fossils have been used as sources of information for palaeontological, palaeocological and palaeoenvironmental analyses. One of the primary interests of vertebrate palaeontologists is the identification of the producer of tetrapod footprints and its contribution to palaeocommunity reconstruction (in conjunction with the bone record), evolutionary studies and potential biostratigraphic implications (e.g., Haubold, 1971, 1984; Lockley, 1991; Lockley and Hunt, 1995; Lockley and Meyer, 2000). Considerable effort has been devoted to the biomechanical and behavioural interpretation of tetrapod trackways using information from biology, laboratory and computational experiments and neoichnological observations on living animals (e.g., McKee, 1947; Padian and Olsen, 1989; Allen, 1997; Gatesy, 2001; Milàn, 2006; Jackson et al., 2010). A less explored source of information

is the use of vertebrate trace fossils as an aid to palaeoenvironmental analysis (e.g., Lockley, 1986; Loope, 1986; Brand and Tang, 1991; Meyer, 1999; Whyte and Romano, 2001; Moratalla and Hernán, 2010; Scott et al., 2012b), description and interpretation of vertebrate ichnofabrics (Tobin, 2004; Melchor et al., 2012c), and the potential distinction of vertebrate ichnofacies (Lockley and Conrad, 1989; Lockley et al., 1994; Hunt and Lucas, 2007).

Lockley (1986) reviewed the use of dinosaur footprints on palaeobiology and palaeoenvironmental analysis. Since the publication of that review, a significant number of contributions emphasizing the use of vertebrate trace fossils in palaeoenvironmental analysis have been published, and also the ichnofacies concept has been applied to vertebrate trace fossils. This contribution builds upon Lockley (1986) and aims to compile and discuss the potential use of various vertebrate trace fossil types, of fish and tetrapod origin, to palaeoenvironmental analysis. The types of vertebrate trace fossils covered in this contribution are: footprints, trails (continuous traces on a bedding plane), burrows, nests, and coprolites. The environmental distribution of

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vertebrate bioerosion trace fossils in bones (like biting and gnawing traces) is poorly known (e.g., Mikuláš et al., 2006), so this type of trace fossils is not considered.

Vertebrate ichnofossils are studied by researchers with different backgrounds and interests. Many studies describe and interpret in detail the trace fossils under a broad stratigraphic and palaeoenvironmental setting, whereas other studies add significant information by including details of the hosting sedimentary facies. The latter studies allow obtaining the maximum palaeoenvironmental information from the vertebrate trace fossils. This procedure can link a particular vertebrate trace fossil to specific environmental parameters.

The applications discussed in this review include: a) identification of tetrapod footprints in cross-sectional views; b) assessment of relative moisture content of different substrates as inferred from the morphology of footprints; c) sand crescents of footprints as indicators of aeolian dune cross-strata; d) identification of pluvial episodes in aeolian dune successions; e) zonation of tetrapod trace fossils in lacustrine margins; f) potential use of flamingo-like footprints in the recognition of alkaline, saline lake facies; g) hippopotamus traces as characteristic of wetlands in arid settings; h) use of vertebrate swim trace fossils to infer water depth, subaqueous substrates and palaeocurrents; i) fish feeding traces as prospective palaeocurrent indicators; j) orientation of tetrapod trackways in comparison with associated primary sedimentary structures; k) the significance of some vertebrate trace fossils for distinguishing perennial from intermittent discharge in fluvial channels; l) significance of vertebrate ichnofabrics; and m) assessment of the utility of vertebrate ichnofacies for palaeoenvironmental analysis.

2. Identification of footprints preserved in cross-section

The recognition of footprints in exposures at high angle to bedding may help to identify subaerially-exposed, or relatively shallow subaqueous intervals, that may be overlooked during sedimentological analysis of sedimentary successions. Footprints in cross section have been recognized in a number of environmental settings including wind-ripple strata of sand flats, interdune and toesets of aeolian dunes (Loope, 1986; Lea, 1996), damp interdunes (Melchor et al., this volume), ephemeral fluvial deposits (Loope, 1986; Smith et al., 1993), floodplain deposits of anastomosed (Nadon, 2001; Difley and Ekdale, 2002) or meandering (Currie et al., 2003) rivers, wetlands (Ashley and Liutkus, 2002; Melchor et al., 2006), and sinkhole deposits (Laury, 1980).

The terminology used by different authors to describe surface footprints and the footprint features observed in cross-section is far from uniform. Allen (1997) proposed a set of terms that are mostly followed here with minor modifications from Jackson et al. (2010) (Fig. 1). The sediment surface directly in contact with the foot is the true track or surface footprint. True tracks may be preserved at nearly the same level that the sediment surface or be limited by sloping track walls, at a depth below the tracking surface. The empty, nearly cylindrical space limited by the track walls is the shaft (also named axis by Fornós et al. 2002), which is recognized in deeply seated footprints produced in cohesive substrates. The track wall may be smooth

or contain striae, which are produced during foot withdrawal. If some sediment adheres to the foot, it may result in a mound projected outside the shaft on the tracking surface, at the anterior part of the footprint. The footprint may exhibit a continuous or discontinuous raised rim, the marginal ridge or marginal upfold, that corresponds with underlying marginal folds and may be limited by a marginal thrust (Fig. 1). Packages of sediment bounded by microfaults that appear in the posterior end of footprints have been termed "pressure pads" (Fornós et al., 2002). Pressure pads are produced when a deeply penetrating limb pivots and creates a backward force to propel the animal forward (Fornós et al., 2002; fig. 21). In practice, pressure pads may be considered a particular type of marginal ridge, and are difficult to distinguish from sand crescents, which are semi-circular mounds of sediment that point downslope in trackways produced on inclined surfaces. Depending upon substrate cohesion, the marginal ridge may be cut by radial tension fractures. In layered sediment, impressions of the foot will be formed in the layers subjacent to the true foot. These impressions have been termed undertracks (Lockley, 1991), undertraces (Allen, 1997) or transmitted (foot)prints (Thulborn, 1990; Romano and Whyte, 2003). Romano and Whyte (2003) used underprint for a case when the rock splits on a surface below the tracking surface, intersecting part of the footprint.

Footprints in cross-section can be distinguished from inorganic deformation structures like convolute bedding, load casts, cryoturbation and ice-wedge thaw structures by a number of criteria (Loope, 1986; Lea, 1996). 1) Footprints tend to be laterally discontinuous in a bed, instead of the laterally repetitive forms of like convolute bedding and load casts. 2) Footprint size distribution displays limited variability and is consistent with potential producers. 3) Footprints display a shaft that may be infilled by texturally different sediment, whereas load structures lack a shaft and are texturally similar to overlying sediments. 4) Downward deformation structures in tightly-packed wind-ripple strata are likely footprints. Wind-ripple strata are not prone to deformation by inorganic processes (such as liquefaction) as are loosely packed grain flow and avalanche strata. Some additional features that apply especially to sauropod footprints include (Difley and Ekdale, 2002; Platt and Hasiotis, 2006): 5) absence of upward mud injection features that are typical of load casts; and 6) the track wall (or the corresponding cast) exhibits grooves and striations as result of digit or claw and skin dragging during withdrawal of foot.

Features for the distinction of footprints from vertebrate burrow fills has been discussed by Lea (1996). Vertebrate burrow fills share with cross-sectional views of footprints the truncation of host strata and may contain a structurally distinct fill. Vertebrate burrow fills usually form inclined cylinders that extend by a distance several times its diameter, whereas footprint shafts are nearly vertical structures that are much shorter than burrow fills. Footprints also lack enlargements and bifurcations that may appear in vertebrate burrow fills. In addition, the host rock adjacent to and underlying a burrow fill commonly is not deformed, although burrow collapse may produce some deformation in the fill of a burrow (Lea, 1996).

3. Relative moisture content of trampled substrates

The surface or cross-sectional features of footprints can help to infer the moisture content of the substrate at the time of their production. The formation of tetrapod footprints is a poorly known subject due to a complex interplay of variables (e.g., Padian and Olsen, 1984; Falkingham, 2014), even if in the last decades there have been a number of studies aiming to ascertain, both qualitatively and quantitatively, different aspects of footprint formation and preservation. The problem has been approached intuitively (Laporte and Behrensmeyer, 1980; Scrivner and Bottjer, 1986; Sarjeant and Leonardi, 1987; Avanzini et al., 2012), through experimental work with live animals (McKee, 1947; Brand, 1979; Brand and Tang, 1991; Brand, 1996; Gatesy et al.,
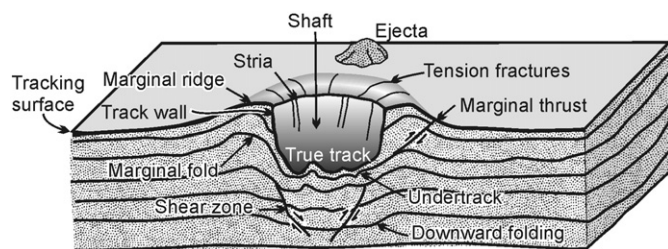

Fig. 1. Block diagram illustrating the morphological features of footprints in cross-section and on bedding plane. Modified from Allen (1997).

1999; Milàn, 2006), and with laboratory–simulated (Allen, 1989, 1997; Manning, 2004; Milàn and Bromley, 2006, 2008; Jackson et al., 2009, 2010; Ellis and Gatesy, 2013) and computer–simulated (Henderson, 2006; Falkingham et al., 2010; 2011) experiments, as well as observations on live animals in natural settings (Cohen et al., 1991; Cohen et al., 1993; Diedrich, 2005; Genise et al., 2009; Marty et al., 2009). A large number of studies have been focused on the behavioural, palaeobiological or biomechanical interpretation of footprints and trackways, but they are beyond the scope of this paper. Every method has advantages and disadvantages. Laboratory– and computer-simulated experiments reduce the uncertainties, but they are at risk of being poor representations of naturally occurring footprints. Field observations of actual animals producing tracks are more realistic, but may include some unknown variables that are difficult to quantify.

The formation and preservation of footprints is directly related to the strain susceptibility of the substrate, the stress produced by the trackmaker (including mass, foot size and shape) and the secondary reworking due to physical and biological factors (see detailed discussion in Cohen et al., 1991). Substrate properties relevant to footprint formation include sediment composition, water content, sediment texture, sediment fabric, cementation, and presence of microbial mats (e.g., Laporte and Behrensmeyer, 1980; Scrivner and Bottjer, 1986; Cohen et al., 1991; Allen, 1997; Graversen et al., 2007; Genise et al., 2009; Marty et al., 2009; Scott et al., 2010). A number of studies have produced information relative to footprint formation on different artificial and natural substrates, including plasticine and mud (Allen, 1997), cement (Milàn and Bromley, 2008), fine-grained sand (Manning, 2004; Jackson et al., 2010), silts (Genise et al., 2009), lacustrine carbonate mud (Scrivner and Bottjer, 1986) and carbonate mud with microbial mats from tidal flats (Diedrich, 2005; Marty et al., 2009). In these studies the sediment consistency and substrate water content was mostly estimated qualitatively, although some studies offered quantitative determinations of water content (Genise et al., 2009; Jackson et al., 2010). Table 1 is a compilation of the morphological details of footprints that can be useful for determination of sediment consistency at the time of footprint formation. Some studies include morphological features of surface footprints (Scrivner and Bottjer, 1986; Allen, 1997; Diedrich, 2005; Genise et al., 2009; Marty et al., 2009) and others provide information on deformation features in undertracks or transmitted footprints, that can be identified in the field in cross-section (Milàn and Bromley, 2008; Jackson et al., 2010). Volcanic ash has been recognized as a substrate with particular properties that affect footprint formation and facilitates early cementation and footprint preservation (Hay and Leakey, 1982; Hay, 1986; Houck et al., 2009; Melchor et al., 2010), although detailed studies on footprint formation in volcanic ash are still lacking. Houck et al. (2009) reviewed Jurassic to Holocene fossil footprints in pyroclastic sediments and highlighted some factors related to their taphonomy and preservation. However, the response of pyroclastic substrates to deformation during footprint formation is unknown to date.

On the basis of studies on fossil footprints preserved in sandstone of aeolian origin, Loope (2006b) argued that tracks associated with fractures (broken laminae), a central shaft and breccia fragments were produced in moist sand. This author argued that, in order for the shaft of the track to remain open after the foot is withdrawn, the sediment must be cohesive. In contrast, tracks lacking a distinctive shaft and with folded laminae, lacking breccias and fractures are indicative of trampling in a dry substrate (Loope, 2006b). Laboratory experiments with dry sand by Jackson et al. (2010) have shown that this distinction remains useful, except that fractures were also formed in dry sand.

4. Tracks with sand crescents as indicators of foreset laminae in aeolian successions

Trackways showing sand crescents that dip in the same direction are indicative of a sloping bedding surface and are related to aeolian dune

cross-strata (Leonardi and Godoy, 1980; Lockley, 1986; Reynolds, 1989; Lockley and Hunt, 1995). Surface sediment bulges or marginal ridges associated with fossil footprints are common, but only on sloping surfaces do the bulges or marginal ridges display the maximum displacement in a single direction (Fig. 2A, B). Sand crescents may be bounded by thrust shear planes that can be identified in cross-section (Fig. 2C–D). Sand crescents can be recognized with confidence in undertracks (Fig. 2B) and even if true tracks are missing due to erosion of overlying laminae (Fig. 3). These eroded tracks may display a distinctive morphology in the form of a unidirectional deformation of the sediments down the palaeoslope (eccentric rings of deformation in laminated sediments) forming a fan of deformation originating from the remnants of the true tracks (Milàn and Loope, 2007).

Fornós et al. (2002) distinguished sand crescents from pressure pads, which were defined as small bodies of microfaulted sediment produced during insertion of the limb in the sediment that may appear on sloping or horizontal bedding planes. In practice, sand crescents may be difficult to distinguish from pressure pads. Identification of tracks with sand crescents in structurally tilted aeolian sandy successions may help distinguishing between sloping dune deposits, and low-angle to flat laying sandstone of low-relief bedforms and sand-flats. Additional features that support an aeolian dune setting for vertebrate trackways with sand crescents are the occurrence of wind ripple cross-strata and/or the presence of arachnid trackways of the ichnogenus *Octopodichnus* in associated low-angle sandstone facies (McKee, 1947; Lockley et al., 1995).

5. Recognition of pluvial episodes within aeolian cross-strata

Highly bioturbated intervals of the Jurassic Navajo Sandstone, USA, have been interpreted as reflecting long-lived pluvial episodes in aeolian deposits (Loope and Rowe, 2003). Aeolian dune and interdune deposits of the Navajo Sandstone near Arizona-Utah border display three heavily bioturbated intervals (bioturbation index between 1 and 5 after Droser and Bottjer, 1986), each up to 25 m thick, which exhibit invertebrate burrows and vertebrate tracks. A 7 m-thick trampled deposit covering a 65 km^2 area was recognized in one of these intervals. Some vertebrate tracks assigned to *Brasilichnium* and *Grallator* lack associated tension cracks or breccias, suggesting that they were made on dry sand (Loope and Rowe, 2003). Preservation of tracks is contrasting in three types of aeolian cross strata. In grainflow deposits tracks are as deep as wide, tracks in thin sets of ripple laminae overlying grain flows are shallower, and tracks are difficult to identify in thick wind-ripple strata. The contrasting preservation is likely related to a greater packing and firmness of wind-ripple laminae compared with loosely packed grain flows. Loope and Rowe (2003) suggested that these bioturbated intervals are a reflection of periods of enhanced rainfall, which fuelled the development of interdune-based ecosystems. Thick bioturbated intervals have not been recorded to date for other aeolian successions.

6. Trace fossil zonation in lacustrine margins

Under this heading, we will discuss 1) two examples of footprint zonation in the margins of modern saline, alkaline lakes (Cohen et al., 1991, 1993; Alonso, 2012), as well as the location of flamingo nest mounds and footprints in the shoreline of the same type of lakes (Scott et al., 2007; 2012b); and 2) two fossil examples including Jurassic lacustrine deposits (Milner et al., 2006) and a Eocene floodplain pond (Genise et al., 2009).

6.1. Modern examples

A shoreline-parallel taphonomic zonation of mammal and bird tracks was identified in the alkaline mudflats of Lake Manyara (Tanzania) by Cohen et al. (1991; 1993). Cohen et al. (1991) distinguished an onshore zone, the strandline zone and a shallow subaqueous

Table 1

Comparison of surface footprints and cross-sectional views of footprints from observations and experiments with different substrate consistency and composition, using animals or a replica of foot. For morphological elements of footprints see Fig. 1.

| Observations, sediment type, footprint morphology	Sediment consistency/water content				
Inferences from fossil footprints, carbonate mud, artiodactyl footprints (Scrivner and Bottjer, 1986)	*Water-saturated* Broad concave-upward impression, marginal ridge, no anatomical detail or faint digit imprints (="squelch marks" of Tucker and Burchette, 1977)	*Water unsaturated* Impressions with pad, digit and internal ridge structures, distorted morphology, marginal ridge or fold (due to flow of mud and sediment adhesion on foot)	*Moist or slightly damp* Shallow well-preserved impressions, sharp hoof outline, high resolution of pad, digit, heel and interdigital ridge, no marginal ridge	*Dry* Shallow footprint, reduced morphological detail and poorly defined outline, no marginal ridge	
Observations on clayey substrates, mammal footprints (Allen, 1997)	*Semi-liquid* No footprint or broad footprint. No marginal ridge, sediment collapse in the shaft	*Soft* Poorly-defined footprint with adhesion spikes, broad marginal ridge cut by radial tension factures, blurred striae in shaft, poor anatomical details	*Stiff* Well-defined footprints, may contain dewclaw imprint, shaft of similar size that footprint, weakly-developed marginal ridge, radial fractures, striated ejecta, good anatomical detail	*Firm* Well-defined shallow footprints, fine anatomical details. Lacking ejecta, marginal ridge and collapsed shaft walls	*Hard* No footprints (scuff marks or broken mud flakes)
Inferences from fossil footprints, carbonate mud, avian footprints (Scrivner and Bottjer, 1986)	*Water-saturated* Highly contorted footprints (flow of mud, deeply penetrating footprints)	*Water unsaturated* Raised plugs of sediment at the joining of three digit imprints, poorly-defined digit outline, partial collapse of mud	*Moist or slightly damp* Well-preserved footprints with sharply-defined digit outlines	*Dry* No footprint formation	
Neoichnological observations on sandpipers (*Calidris* spp.) in subaqueous and subaerial sandy siltstone from a pond mudflat (Genise et al., 2009).	*Subaqueous semi-liquid substrate, moderate organic content (WC: 48-85%, OM: 1.4–1.8%)* Very poorly-defined impression with blurred or collapsed digit imprints	*Subaqueous soupy substrate with algal mat (WC: 50%, OM: 1%)* Very well-defined tridactyl footprints	*Subaerial wet substrate (WC: 20-35%, OM: 0.25-0.9%)* Very well-defined tridactyl footprints with pad impressions	*Subaqueous wet substrate, no algal mat (?) (WC: 18-22%, OM: 0.2-0.5%)* Tridactyl footprints with poorly-defined thin digit imprints	*Dry sediment recently flooded (WC: 28%)* No footprint formation
Experiments with layered cement using a tridactyl foot of a emu (Milàn and Bromley, 2008))	*Semi-liquid* Distorted, very low-relief surface track, claw disrupts laminated cement, flow of material over digits	*Soft* Poorly-defined surface track, undertrack retains the shape of foot. Collapse of track walls above digits, material dragged during withdrawal, raised rim around exit hole of digit III	*Moist* Surface track with slender digit impressions (collapse after withdrawal) although claw and pad impressions are distinguished, undertracks are shallower and wider than surface tracks	*Firm* Well-defined footprints showing high quality of anatomical details (claws and pads, no skin impression). Adhesion spikes, digits appears wider and more rounded undertrack	
Experiments with fine sand and 20% cement, rubber replica of pes of the onithopod dinosaur *Hypsilophodon foxii* (tetradactyl: I-IV) (Jackson et al., 2010)	*Saturated (WC: 30%)* Distorted tetradactyl footprint (up to 20% larger than foot), sediment collapse and water infilling after foot withdrawal, footprint margin indistinct. Chaotic mix of liquified sediment below surface track, displacement bulbs below digit imprints. Foot penetration depth up to 57 mm	*Moist (WC: 20%)* Shallow surface tridactyl track (II-IV), good anatomical detail (pads, claws), only slightly larger than foot. No sediment collapse or marginal fold. Transmitted track 50% larger than foot. Low-amplitude downward folding up to 70 mm below footprint. Foot penetration depth 11 mm	*Moist (WC: 10%)* Shallow surface tridactyl track (II-IV), good anatomical detail (pads, claws), only slightly larger than foot. No sediment collapse or marginal fold. Transmitted track 20% larger than foot. Low-amplitude downward folding up to 75 mm below footprint. Foot penetration depth 7 mm	*Dry (WC: 0%)* Spur-like structure due to flow and collapse after withdrawal, tetradactyl track, marginal ridge related to thrusting, extensional shear zones below track. Foot penetration depth 30 mm	
Observations on the formation of human footprints in present-day algal mats on carbonate tidal flats (Marty et al., 2009)	*Water saturated mat* In thin mats: poorly-defined surface footprint. In thick mats: gross outline of footprint preserved only if underlying sediments are water saturated	*Water unsaturated mat* Thin and thick mats: large morphological variety of footprints. Well-defined footprint with good anatomical details and marginal ridge only if underlying sediment of high yield strength	*Moist mat* In thin mats: shallow well-defined footprint with anatomical details, only if overlying sediment with moderate yield strength. In thick mats: shallow and less-defined footprints	*Dry mat* In thin mats: poorly-defined footprint, mat cracking (over soft sediment) or no footprint (over sediment of high yield strength or mat of high elasticity). In thick mats: broadly-defined footprint only if underlying sediment is soft	
Neichnological experiments on a carbonate tidal flat with a live Iguana (Diedrich, 2005)	*Soupy to semi-liquid subaerial to shallow subaqueous mud* Not very well-preserved footprint, digit reduction, elongated swim marks	*Wet mat (soft carbonate mud)* Shallow well-preserved footprints (including digital pads and scale impressions)	*Slightly wet mudcracked mat* Claw marks (parallel scratch marks from body skin)	*Dry mudcracked mat* No footprints or only claw marks	

WC: water content; OM: organic matter content.
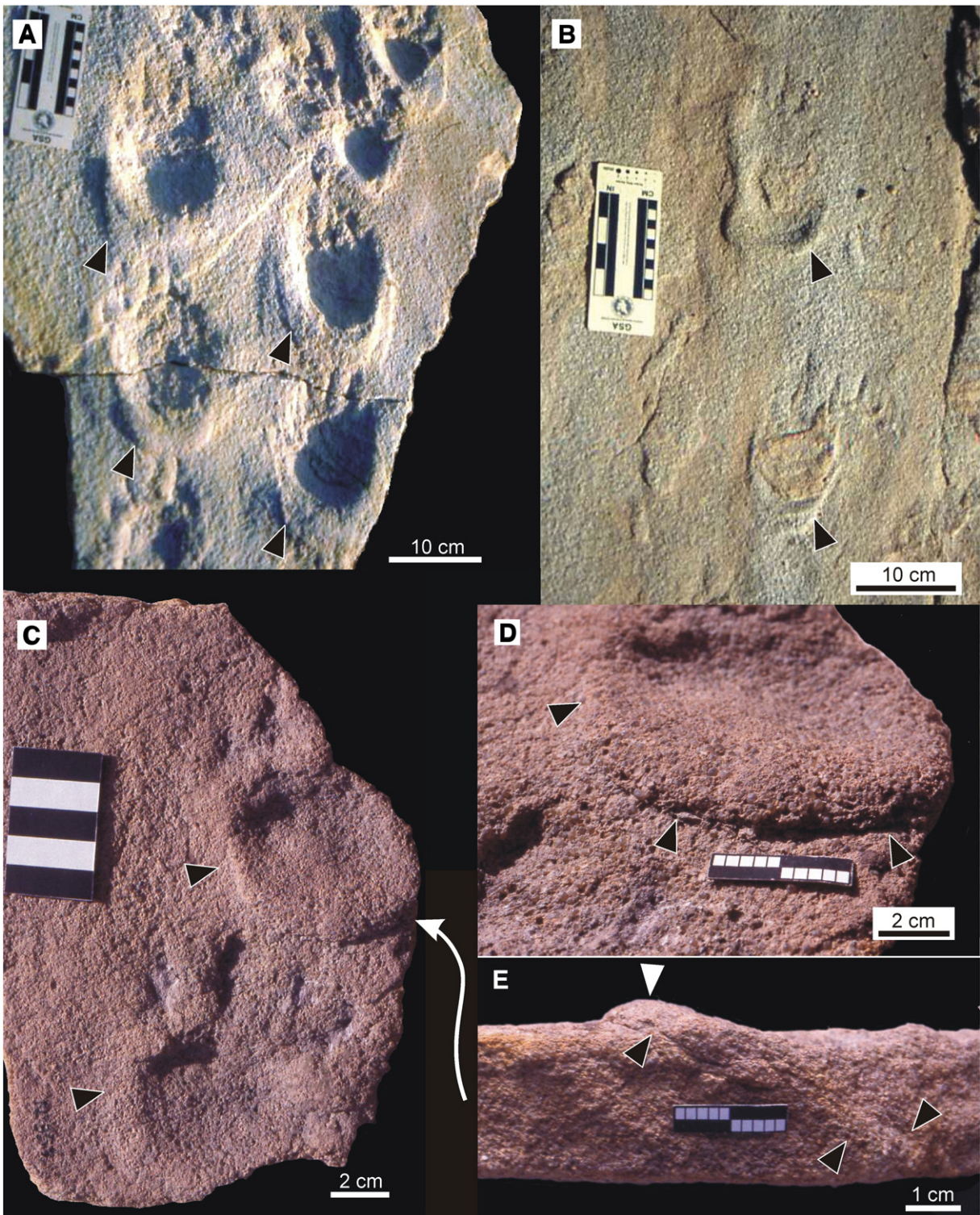
Fig. 2. Trackways and footprints of the ichnogenus *Chelichnus* showing sand crescents, from the Early Permian Yacimiento Los Reyunos Formation of Mendoza province, Argentina. (A) Trackway with surface footprints and sand crescents (arrowed) pointing downslope. (B) Undertracks with poorly developed sand crescents (arrows). (C) Pair of footprints with clear sand crescents (black arrows). (D) Oblique view of the upper footprint of Figure C with a close-up of the sand crescent and thrust plane (arrows). (E) Transverse view of the slab of Figure C (pointed area), showing the outline of the sand crescent (white arrow) and the bounding thrust planes (black arrows). Figures C-E are from specimen MMHNSR/PV 359 from the Museo Municipal de Historia Natural de San Rafael, Mendoza province, Argentina.

zone, whose physical properties are controlled by the water content of the sediments (a mixture of carbonate detritus and terrigenous silts). The onshore zone of the lake mudflat contains dry sediments and moderately thick evaporite crusts and is subject to wind deflation. Groundwater fluctuation and invertebrate bioturbation have minimal effects on the onshore zone. The onshore zone only displays footprints

of large mammals (mainly ungulates) that are not morphologically distinctive, and can deform by sun baking, cracking and salt efflorescence (Scott et al., 2010). The strandline zone of the lake mudflat contains fine-grained saturated sediments; and it is characterized by near-surface groundwater fluctuations, onshore seiche events, intense vertebrate trampling and invertebrate bioturbation. Wind deflation is
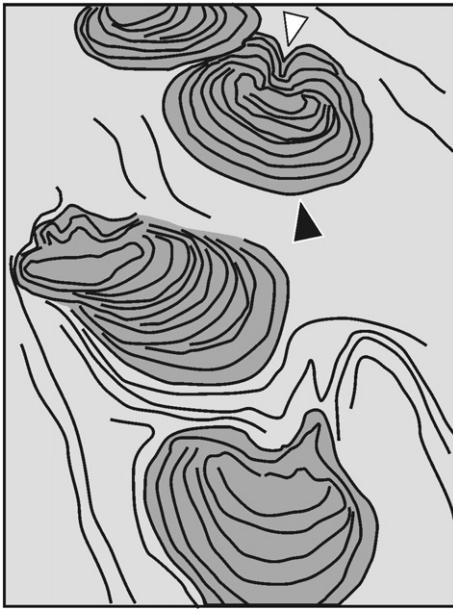
Fig. 3. Diagram of four eroded tridactyl footprints with sand crescents (black arrow) illustrating the utility of these structures to identify sloping aeolian dune deposits. The white arrow indicates the approximate position of digit III. Modified from Milàn and Loope (2007)).

minimal and evaporite crusts and mudcracks are usually absent in this zone. The strandline zone is relatively narrow and distinguished by well-preserved bird and small mammal footprints, along with large mammal footprints (Cohen et al., 1993). The shallow subaqueous zone contains soupy sediments that are not subject to the formation of evaporite crusts, deflation or invertebrate bioturbation. In this zone, there are poorly-defined and large tracks showing fewer morphological details than in the remaining zones. The tracks of smaller animals are not preserved in the shallow subaqueous zone either due to water depth or destruction by liquefaction (Cohen et al., 1991; 1993). In the strandline and shallow subaqueous zones, mammal trackways displayed a preferential bimodal orientation, both shore parallel (the dominant) and shore normal (Cohen et al., 1993).

A separate example of zonation in modern borate-bearing alkaline lakes is that described by Alonso (1987, 2012) from the Laguna de los Pozuelos of Jujuy province, northwest Argentina. This lake is a potential modern analog of continental borate deposits (Alonso 2012). On the basis of an observed preferential spatial distribution of avifauna in that lake (Mascitti and Castañera, 1991), a hypothetical zonation of bird track types for a shallow borate-bearing lake has been proposed (Alonso 2012). The track zones are: 1) terrestrial to emergent mudflat (sand and silt), dominated by tetradactyl bird tracks with marked phalangeal pads (mainly Passeriformes, occasionally Rheiformes); 2) submerged mudflat to shallow littoral (silt and clay), characterized by tridactyl bird tracks, including small palmate tracks (assigned to Charadriiformes and Anseriformes); and 3) a deeper littoral zone (clay and evaporite muds), characterized by large palmate bird tracks (comparable with those of Phoenicopteriformes and Anseriformes). These three zones cover a water depth range from subaerial to 0.5 m deep. Further studies are necessary to confirm if this zonation can be applied to other saline, alkaline lakes and fossil examples.

Modern (as well as Holocene and Pleistocene) sediments in the margins of hypersaline, alkaline Lake Bogoria and Lake Magadi (Kenya), contain flamingo nest mounds and trampled grounds that are considered good indicators of the shoreline or very shallow water (Scott et al., 2007; 2012b). Breeding flamingos typically construct conical nests with flattened tops (about 30 cm wide and 20 cm high) using wet mud in very shallow water (lake mudflats and low-gradient subaerially exposed delta front). Flamingo nest mounds are composed

of siliciclastic muds and are internally massive or show ped-like structure, which distinguishes them from thrombolites that are composed of carbonate and show a clotted mesoscopic fabric (Scott et al., 2012b). Trampling by flamingos in lake margin settings also produces distinctive surfaces that may appear more compacted that the surrounding substrates (Scott et al., 2007; 2012b).

6.2. Fossil examples

In the fossil example of the Lower Jurassic lacustrine deposits of the Moenave Formation of Utah (Milner et al., 2006), the distribution of walking and swim traces and associated sedimentary structures allowed distinguishing the approximate location of the shoreline. Onshore locations (emergent lake mudflat) are distinguished by the presence of walking footprints of small and large theropods accompanied by physical indicators of emergence and evaporation (mudcracks, raindrop imprints and sulfate salt crystal casts). The subaqueous onshore area is distinguished by swim traces of small theropods (ichnogenus *Characichnos* Whyte and Romano 2001), large theropod footprints, wave and current ripples, and surface invertebrate trails (Milner et al., 2006).

Late Eocene pond deposits from northwest Argentina (Melchor et al., 2002; Melchor et al., 2013a; Vizán et al., 2013) contain hundreds of small avian footprints assigned to *Gruipeda dominguensis* de Valais and Melchor, 2008. A modern analog is a coastal pond in the Chubut province, southern Argentina, where Genise et al. (2009) documented footprint formation and behaviour of extant sandpipers (*Calidris* spp.). The Late Eocene deposits accumulated in a small (a few square meters), shallow pond of sheetflood origin, which was emplaced in a low-relief landscape (Melchor et al., 2006). Using footprint density and morphology and physical sedimentary structures, three areas were recognized in the fossil example; a central area, the shoreline, and onshore zone (Fig. 4). All of these contained *G. domiguensis* footprints. The central area is typified by a high density of poorly defined footprints, where trackways can not be distinguished, and the footprints are the deepest. The uppermost tracked sediment is covered by a thin mud drape. This area is interpreted as the deepest part of the pond, which remained subaqueous, allowing settling of mud from suspension and foraging activities by birds. The fossil shoreline is distinguished by shallow and well-defined footprints of moderate density, clear trackways oriented parallel and perpendicular to the boundary of the area, presence of landing traces (similar to *G. dominguensis* with very long digit I imprints), and a very thin mud drape (Fig. 4). The inferred onshore zone of the Late Eocene pond is characterized by the presence of very well-defined and shallow footprints with pad and claw impressions and thin digits, composing a few isolated trackways (low footprint density), and pecking marks (Fig. 4). The bedding surface is either flat-bedded or contains current ripples; in addition, wrinkle marks and a very thin or absent mud drape were noted. The onshore zone was subaerial most of the time but no mudcracks were developed, due to the inferred short lifetime of the fossil pond (Genise et al., 2009).

7. Flamingo-like tracks as indicators of saline, alkaline lakes

The presence of abundant flamingo-like tracks in post Oligocene successions has been proposed as a good indicator of saline and/or alkaline waters in lacustrine deposits (Melchor et al., 2012a). This relationship is inferred from the specialized filter-feeding mechanism of Late Oligocene to modern flamingos and their common flocking behaviour (e.g., Chapman, 1905; Jenkin, 1957). The tracks of the modern Chilean flamingo (*Phoenicopterus chilensis*) are tridactyl, palmate, wider than long, and with a distinctive asymmetrical rounded proximal end defined by the curved impression of digits II and IV (Fig. 5A). The imprint of the interdigital web does not reach the termination of the digit III impression, and the interdigital angle between digit imprints II-III is commonly smaller than those of
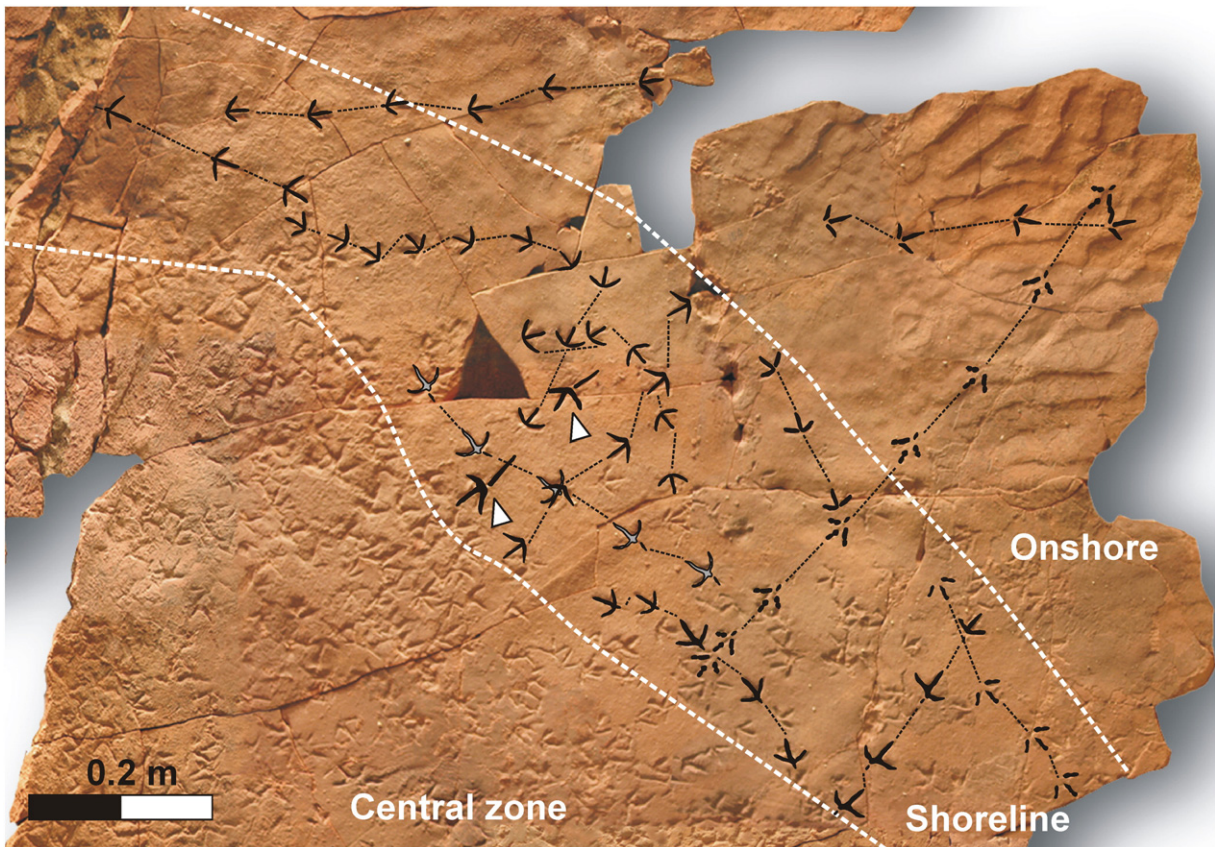
Fig. 4. Mosaic of slabs from a pond deposit of the Late Eocene Laguna Brava Formation (northwest Argentina). Dashed lines indicate the approximate boundary of the pond zones as inferred from features of bird footprints and sedimentary structures. Footprints composing discrete trackways are highlighted. Bird footprints with elongated hallux imprints (landing traces) are indicated by arrows. Modified from Genise et al. (2009).

digits III-IV, which makes the impression asymmetric (Melchor et al., 2012a). The ichnogenera *Phoenicopterichnum* Aramayo and Manera de Bianco, 1987 (Figs. 5B, C); *Presbyorniformipes* Yang et al., 1995; and *Culcitapeda* Sarjeant and Reynolds, 2001 are regarded as sharing a common morphology typical of modern flamingo footprints (Melchor et al., 2012a). Case studies where flamingo-like footprints are associated with saline or alkaline waterbodies are the Late Pleistocene-Holocene sediments of Lake Bogoria, Kenya (Scott et al., 2007; 2009; 2012a); the Late Miocene to Pliocene Río Negro Formation of southern Argentina (Aramayo, 2007; Melchor et al., 2013b); the Late Miocene Sijes and the Pleistocene Blanca Lila Formations of northwest Argentina (Alonso, 1987, 2012); the marginal marine pan sediments of the Miocene Upper Red Formation of Iran (Abbassi and Shakeri, 2005); and probably the late Pliocene Gila Conglomerate of Arizona, USA (Thrasher, 2007).

Alonso (1987, 2012) argued that some fossil avian tracks can be a useful indicator of borate deposits. One of the most characteristic avian tracks in these environments are those of Phoenicopteriformes (flamingos), which are particularly abundant in mudflats and salt pans of saline, alkaline lake deposits (e.g., Alonso, 2012; Scott et al., 2012b). In particular, Alonso (2012) noted that avian tracks in borate deposits occur along with gypsum, wave ripples, travertine and different borate minerals. Known borate deposits are found in Miocene and younger sequences and their occurrences are typified by closed lake basins, arid climate with coeval explosive volcanism and active hydrothermal groundwater sources. The relationship between borate deposits and diverse avian tracks was noted in the late Miocene Sijes and Pleistocene Blanca Lila Formations of northwest Argentina and in the middle Miocene Horse Spring Formation (Nevada) and Miocene Tropico Group (California) of southwestern USA (Alonso, 1987; Ortí and Alonso, 2000; Alonso, 2012).

8. Hippopotamus traces and freshwater wetlands of arid basins

Deocampo (2002) demonstrated that Neogene to modern freshwater wetlands may exhibit a set of tetrapod traces, mainly hippopotamus traces that are distinctive of freshwater wetlands. This is due to the strong dependence of extant and fossil Hippopotamidae on freshwater bodies. The set of traces includes a central, up to 2 m thick, bioturbated massive deposit (hippopotamus pool), surrounded by radiating or dendritic hippopotamus trails. The latter are parallel to lake shoreline and shallow toward distal positions, where individual footprints become discernible. A higher diversity of footprint types as well as easily distinguished individual footprints can be found in surrounding deposits. Hippopotamus trails are U-shaped structures about 1–5 m wide and 0.5-1 m deep bounded by lateral levees, that are infilled with either organic-rich spring sediments or lacustrine muds (Ashley and Liutkus, 2002; Deocampo, 2002). Hippopotamus trails can be distinguished from potentially similar structures produced by fluvial scouring or channelization by a massive and fine-grained fill and a lower, gradational infill (Deocampo, 2002). Fossil hippopotamus trails have been recognized in the Pleistocene deposits of Olduvai Gorge, Tanzania (Ashley and Liutkus, 2002; Fig. 7). A further potential example are unusually narrow (1–2 m wide and 1 m deep) incisions in river channel bank and levee deposits of the Lower Eocene Willwood Formation in the Big Horn Basin of Wyoming (Ashley and Liutkus, 2002).

On the basis of the known influence of hippopotamus trails on the location of channels of the modern Okavango fan (McCarthy et al., 1998), it has been hypothesized that dinosaur trails might have influenced the location of ribbon channels in the Upper Jurassic Morrison Formation of Utah (Jones and Gustason, 2006).

Structures similar to hippopotamus trails produced by sauropod dinosaurs have been described from the Lower Cretaceous lagoonal
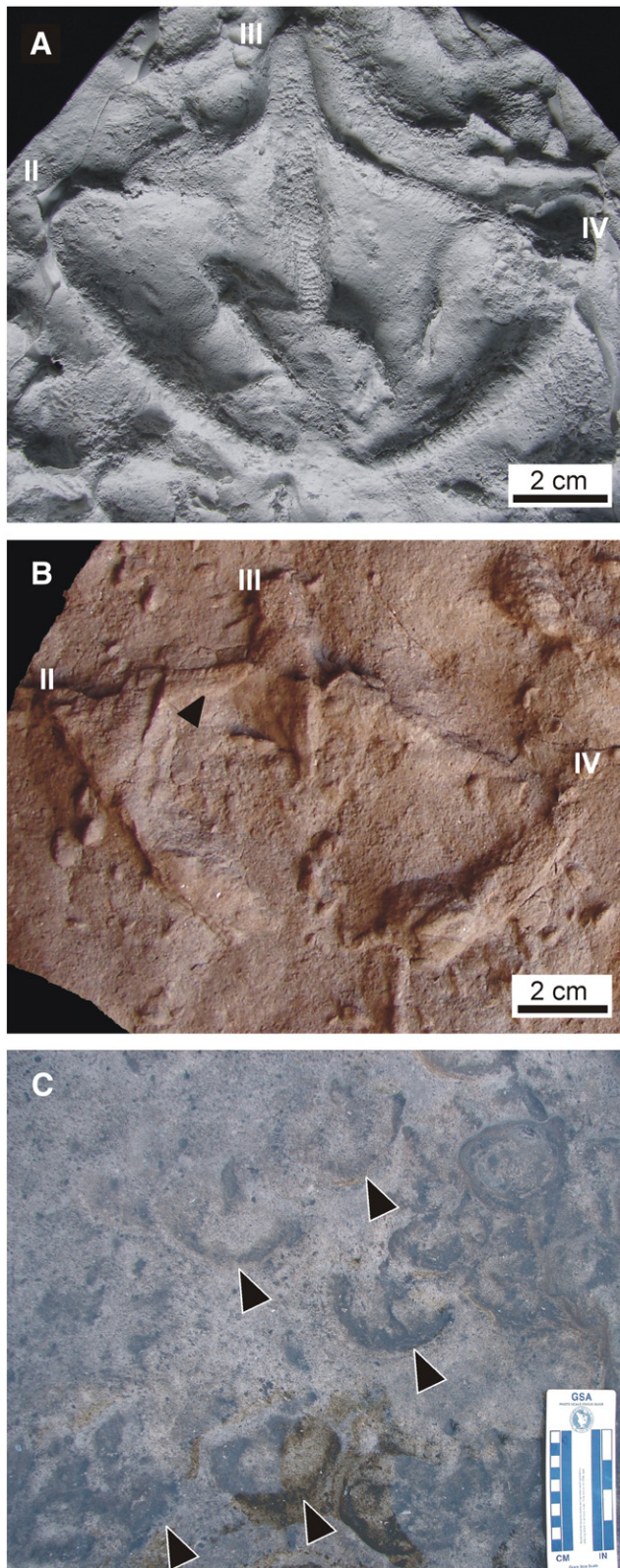
Fig. 5. Modern flamingo and fossil flamingo-like footprints. (A) Cast of a left pes of *Phoenicopterus chilensis* (specimen GHUNLPam 12212, from the Palaeontology Collection of the Facultad de Ciencias Exactas y Naturales, Santa Rosa, La Pampa, Argentina). (B) *Phoenicopterichnum* isp. preserved as positive hyporelief from the Oligocene-Miocene Vinchina Formation of northwest Argentina. (C) Several *Phoenicopterichnum* isp. (arrows) in a moderately dense array of footprints as typical of lacustrine shorelines. Field photography from the Late Miocene Río Negro Formation, Río Negro province, Argentina. II to IV indicates the imprints of digits II to IV. Figures A and B modified from Melchor et al. (2012a).

deposits of western Australia (Thulborn, 2012). These are very large trough-like features that are several meters wide and up to 20 m long or more, which contain scattered sauropod footprints or trackways. These structures have been named "dinosaurian thoroughfares" and are flanked by areas of untrodden substrate where tracks of smaller tridactyl dinosaurs occasionally appear (Thulborn, 2012). Thulborn (2012) suggested that the lagoonal substrates were fairly firm and stabilized by algal mats and that the repeated passage of large sauropod dinosaurs produced the deformation and areas of preferential compaction.

9. Vertebrate swim trace fossils

Traces interpreted as reflecting tetrapod swimming behaviour are commonly characterized by groups of up to 5 subparallel ridges (or furrows) lacking the impression of the autopodium. These traces may compose an irregular trackway or, more commonly, cover complete bedding planes in a confused array (e.g., Boyd and Loope, 1984; Whyte and Romano, 2001; Lockley et al., 2014). One of the common features of tetrapod swim traces is that the individual ridges decrease in height backward as a result of the raking or paddling movement of the producer (e.g., McAllister, 1989; Lockley et al., 2014). Other features that may be useful to infer the orientation of the producer is the presence of a shallow mound and/or occasional reflexures in the back of the set of imprints (Fig. 6A) (Boyd and Loope, 1984). Swim traces have been assigned to different tetrapod groups including non-avian theropod dinosaurs (Fig. 6A), crocodiles (Fig. 6B), turtles (Fig. 6C), pterosaurs (Fig. 6D), small amphibians (Fig. 7), and aquatic mammals (hippopotami).

Fish swim traces are also distinctive. These trace fossils are essentially recognized as the ichnogenus *Undichna* Anderson, 1976 (Fig. 7), which is composed of paired or unpaired, continuous sinusoidal trails that may be in phase or out of phase (e.g., Higgs, 1988; Trewin, 2000; Minter and Braddy, 2006; Cardonatto and Melchor, 2014).

Three major sources of information for palaeoenvironmental interpretation include; 1) inferences about absolute value and range of variation of water depth (mostly from bipedal dinosaur swim traces), 2) the subaqueous nature of the substrate (crocodile, turtle, fish and hippopotamus swim traces) and 3) current directions.

9.1. Water depth

Theropod swim traces comparable to *Characichnos* have been used to estimate water depth at the time of trace formation in Jurassic-Cretaceous fluvial deposits (Whyte and Romano, 2001; Romilio et al., 2013; Xing et al., 2013). The basic assumption in these examples is that the dinosaurs were buoyant and barely touched the bottom, and that water depth can be approximated by the height at hip (h, or total hind limb length) of the producer (Fig. 8). Height at hip can be estimated using footprint length (FL) from tridactyl walking tracks that are of similar width to the swim traces and, preferably, appear in the same sedimentary sequence (Whyte and Romano. 2001). For theropods, some of the proposed estimates are h ≈ 4.6 FL, if FL is less 25 cm, and h ≈ 5.7 FL, if FL is greater than 25 cm (Thulborn, 1990). These estimates have been re-evaluated using computer models (Henderson, 2003). When the presumed producer of the swim traces is known, h can be estimated from the sum of the lengths of femur, tibia and longest metatarsal, plus an increment of 9% to account for ankle bones and for soft tissues (Thulborn, 1982).

Estimates of water depth of lacustrine deposits were accomplished using pterosaur swim traces on wave rippled bedding planes of the Cretaceous Dakota Group (Lockley et al., 2014), assuming that pterosaurs were floating in shallow water while touching the subaqueous substrates (Lockley and Wright, 2003).
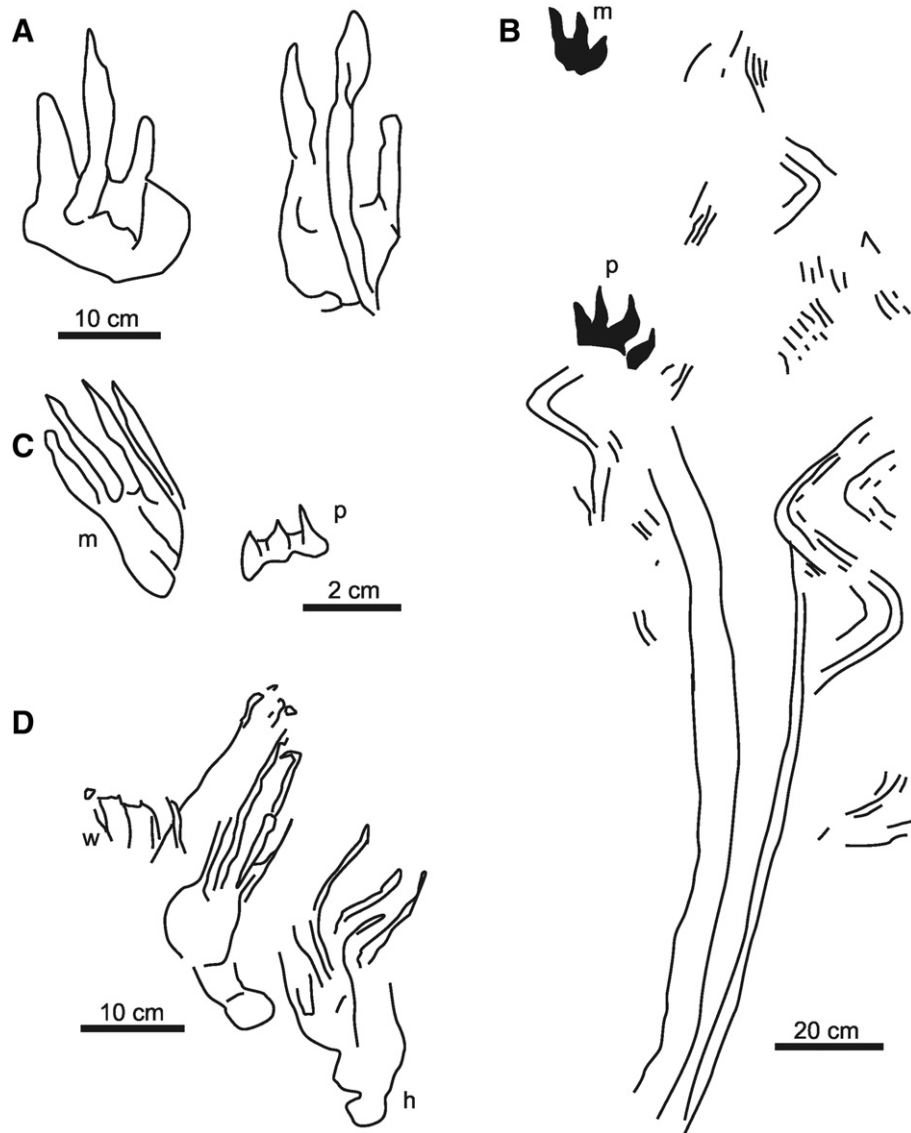
Fig. 6. Examples of fossil tetrapod swim traces. (A) Theropod swim traces (*Characichnos*) from Middle Jurassic crevasse-splay deposits of UK. Modified from Whyte and Romano (2001). (B) Crocodile swim trace (*Hatcherichnus*) from the Upper Jurassic Morrison Formation of USA. Modified from Foster and Lockley (1997). (C) Manus-pes couple of turtle swim traces from the Upper Jurassic Lastres Formation of Spain. Modified from Fig. 4 of Avanzini et al. (2005). (D) Pterosaur swim traces from the Cretaceous Dakota Group of USA. Modified from Lockley et al. (2014). m: manus, p: pes, w: web traces, h: heel trace.

Additionally, the joint occurrence of swim and walking traces on the same bedding plane indicates that the water depth changed during the formation of the tracking surface. This information cannot be inferred from any other physical sedimentary structure. Some examples of this inference include: 1) a Permian lacustrine dolomite from Oklahoma (USA), which contains swim and wading traces of small reptiles or amphibians (Swanson and Carlson, 2002; 2) Lower Cretaceous fluvial deposits from China with theropod swim (*Characichnos*) and walking traces (Xing et al., 2013; 3) Lower Cretaceous lacustrine deposits from China with walking and swim traces (including tail traces) assigned to ornithopods (Fujita et al., 2012); 4) Albian–Cenomanian marginal marine deposits from Utah, USA (Anfinson et al., 2009); and 5) Albian–Cenomanian fluvial floodplain deposits from Australia with half-swimming and walking trackways assigned to ornithopods (Romilio et al., 2013). In the case study from Australia, the depth range estimated for the water body during formation of the track surface ranged between 0.14-1.60 m (based on the height at hip estimated for the purported producers; Romilio et al., 2013).

9.2. Subaqueous substrates

Crocodilian, turtle, amphibian and hippopotamus swim traces are not adequate to estimate the water depth because of the known bottom walking (or punting) and swimming habits of these groups (e.g., Brand, 1979; Bennett et al., 2014; Lockley et al., 2014). Instead, they are very good indicators of subaqueously-deposited substrates, as are fish swim trace fossils. Mesozoic crocodilian swim traces have been recognized under the ichnogenera *Hatcherichnus* Foster and Lockley, 1997 (Fig. 6) and *Characichnos* (Lockley et al., 2010; Vila et al., 2015), whereas Cenozoic crocodilian swim or basking traces were recognized under three separate ichnogenera (see Lockley et al., 2010). The presence of crocodilian tracks may be used to indicate aquatic tropical and subtropical environments, including deltas, lakes, large river systems, and diverse coastal plain environments, according to the present distribution of representatives of the group (Lockley et al., 2010). *Hatcherichnus* was reported in fluvial deposits of the Upper Jurassic Morrison Formation, USA, in Upper Jurassic deltaic and coastal facies of the Lastres Formation of Asturias, Spain, and in fluvial, delta plain and estuarine
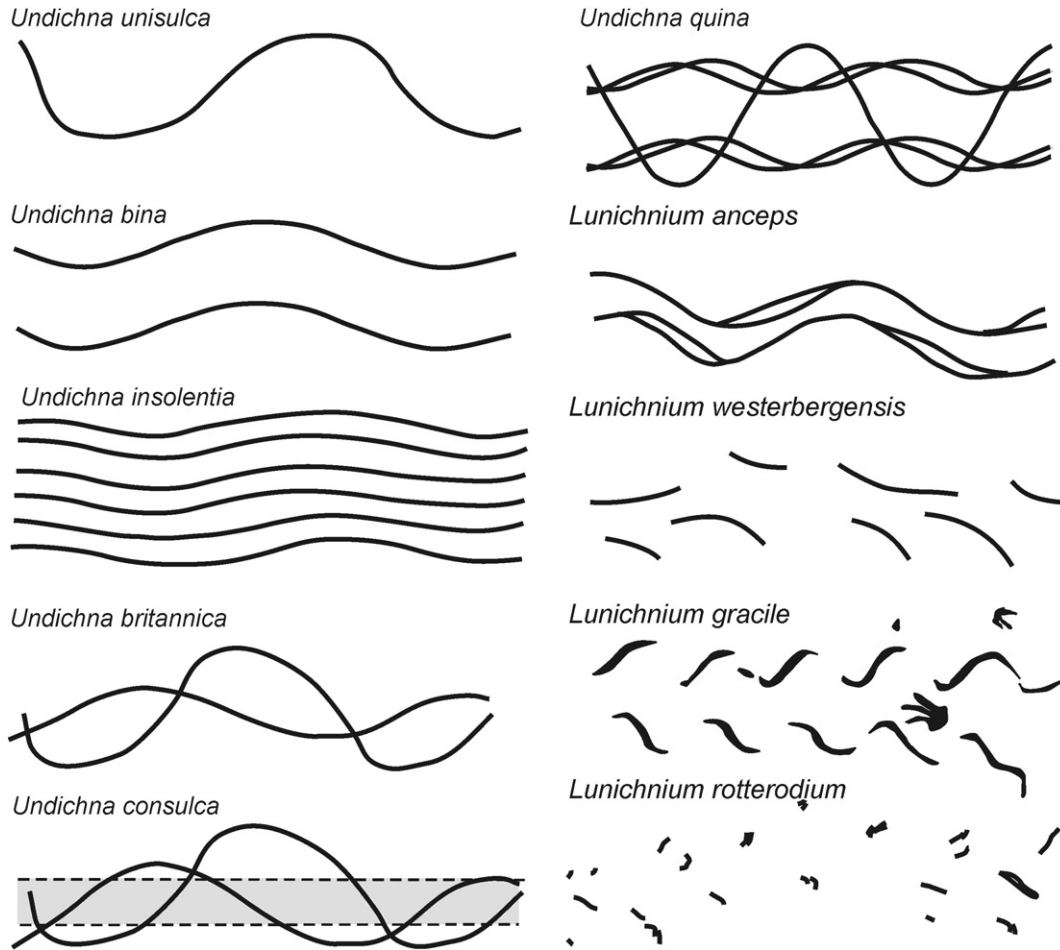
Fig. 7. Morphology of the main ichnospecies of fossil fish and amphibian swim traces. *Undichna* ichnospecies modified after Cardonatto and Melchor (2014). *Lunichnium* diagrams after Walter (1983; *L. rotterodium*), Turek (1989; *L. anceps* and *L. gracile*) and Minter and Braddy (2006; *L. westerbergensis*).

deposits of the Middle Cretaceous Dakota Group of Colorado, USA, (Foster and Lockley, 1997; Avanzini et al., 2007; Lockley et al., 2010).

Turtles are capable of two types of aquatic locomotion (Zug, 1971): bottom walking and true swimming, depending if the limbs touch or are not in contact with the bottom, respectively. Turtles produce wide trackways as a consequence of their sprawling stance (Avanzini et al., 2005). Turtle bottom–walking trackways have tridactyl to pentadactyl prints with a digitigrade manus that is wider than long and a semi-plantigrade to plantigrade pes showing elongated digit imprints (Foster et al., 1999; Avanzini et al., 2005; Lockley et al., 2014). A recent
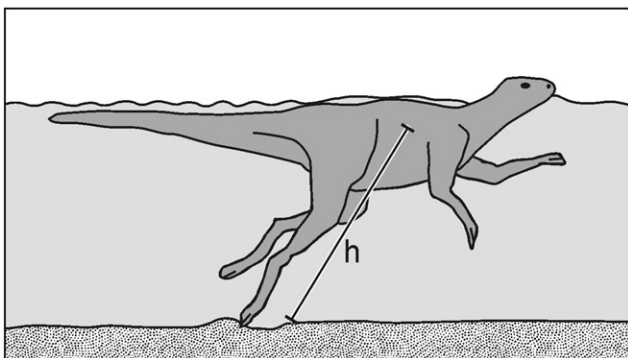

Fig. 8. Diagram of a buoyant bipedal dinosaur during swimming. h: height at hip (proxy for water depth). Modified from Whyte and Romano (2001).

review (Avanzini et al., 2005), suggests that the only valid ichnogenera of turtle tracks (which may include bottom walking and terrestrial walking traces) are *Chelonipus* Rühle von Lilienstern, 1939 and *Emydhipus* Fuentes Vidarte et al., 2003. Bottom-walking trackways are distinguished from terrestrial walking turtle trackways on the basis of incomplete footprint sequence, especially on one side, and elongated ungual scratch marks (Foster et al., 1999; Avanzini et al., 2005).

Amphibian swim traces display a combination of continuous and discontinuous sinusoidal trails associated with scattered partial or complete footprints (Walter, 1983; Turek, 1989; Minter and Braddy, 2006). These traces are morphologically akin to *Undichna*, although the occasional occurrence of footprints is one of the main clues for the amphibian origin. Amphibian swim trace fossils are commonly discontinuous trails, instead of the essentially continuous trails typical of fish swim trace fossils. Late Palaeozoic amphibian swim traces have been mostly assigned to two ichnogenera: *Lunichnium* Walter, 1983 (Fig. 7) and *Serpentichnus* Braddy et al., 2003 (e.g., Turek, 1989; Minter and Braddy, 2006).

Hippopotamus bottom walking or punting (underwater gait mode consisting in limbs pushing off the substrate producing alternating phases of thrust and glide) traces have been described from the fluvial-lacustrine deposits of the Pliocene-Pleistocene Koobi Fora Formation, Kenya (Bennett et al., 2014). These traces appear on the same surface, although at a distance of tens of meters, where hominin and normal walking hippopotamus tracks occur, confirming footprint formation in a subaqueous substrate as originally interpreted by Behrensmeyer and Laporte (1981).

9.3. Current directions

Assemblages of dinosaur swim traces in shallow lacustrine and fluvial deposits of Mesozoic age display an average orientation opposite to associated primary sedimentary structures. Examples include: 1) Lower and Middle Triassic fluvial, deltaic and coastal deposits from USA (Boyd and Loope, 1984; Thomson and Lovelace, 2014), 2) Middle Jurassic crevasse-splay deposits from UK (Whyte and Romano, 2001), and 3) Cretaceous tidally-influenced fluvial deposits from USA (Lockley et al., 2014). A floating animal moving downstream will barely touch the bottom; this is a likely explanation for the preferential preservation of traces produced by tetrapods swimming upstream (Boyd and Loope, 1984).

10. Fish feeding traces as palaeocurrent indicators

Fish feeding trace fossils (or their modern counterparts) have been mostly referred to the ichnogenera *Piscichnus* Feibel, 1987 (e.g., Howard et al., 1977; Gregory, 1991; Pearson et al., 2007) and *Osculichnus* Demírcan and Uchman, 2010. Other fish feeding structures include ellipsoidal traces associated with *Undichna* (Martin et al., 2010) and modern *Cruziana*- and *Rusophycus*-like traces (Muñiz et al., this volume). Certain modern fish feeding traces are oriented with the predominant current and hold the potential of being useful palaeocurrent indicators in intertidal settings. These traces are shallow depressions interpreted as ray feeding traces from estuarine sand bars and tidal flats of Georgia, USA (Howard et al., 1977) and roughly similar structures produced by the Atlantic sturgeon in intertidal mud flats of the Bay of Fundy, Canada (Pearson et al., 2007). Both are morphologically comparable with the ichnogenus *Piscichnus*. The traces of the Georgia coast are circular to ovate depressions ranging from 6 cm to 1 m in diameter with the up current margin undisturbed and with shallow arcuate mounds in the downcurrent side. The depressions are up to about 30 cm deep, with steep walled margins (Gregory, 1991). These traces are mainly produced during ebb tide and usually appear in large numbers (Howard et al., 1977; Gregory et al., 1979).

Typical sturgeon feeding excavations from the Bay of Fundy are composed of a shallow, crescent-shaped snout impression (of poor preservation potential) adjacent to a cylindrical plug-shaped excavation 5–15 cm in diameter, and 2–6 cm deep (Pearson et al., 2007). Sturgeons must orient with prevailing hydraulic currents to maintain stability during feeding. Pearson et al. (2007) found that sturgeon feeding traces are predominantly oriented at two prevailing and opposing orientations that correspond with excavations made during flood and ebb currents.

11. Tetrapod trackways as palaeocurrent indicators

Most dinosaur trackways in lacustrine deposits are either shore parallel (more common) and shore normal, whereas non-dinosaurian trackways in fluvial floodplain deposits match palaeocurrent data derived from sedimentary structures. Dinosaur trackways in lacustrine carbonate and siliciclastic deposits commonly are oriented parallel to the shoreline as inferred from facies patterns or wave ripple crests. Well known examples with a large number of measured trackways include: 1) the Upper Jurassic Morrison Formation of Colorado, USA, with trackways assigned to sauropod and ornithopod dinosaurs (Lockley et al., 1986; Schumacher and Lockley, 2014); 2) the Berrasian Huérteles Formation of the Cameros Basin, Spain, comprising trackways essentially produced by theropods (Moratalla and Hernán, 2010); and 3) the Upper Cretaceous El Molino Formation of Bolivia, with trackways assigned to sauropod and ornithopod dinosaurs (Meyer et al., 2001). All of these examples were produced in lacustrine mudflats with dominantly carbonate sedimentation. The example of shore-parallel trackways in siliciclastic lacustrine settings is the Lower Cretaceous Sousa Formation of Brazil, which is dominated by theropod footprints along with footprints of sauropod and ornithopod dinosaurs

(Leonardi, 1994). A further example –shallow lacustrine to mudflat siliciclastic deposits of the Upper Cretaceous Jindong Formation of Korea– suggests a preferential orientation of sauropod and ornithopod dinosaur trackways at a high angle with the wave ripple crests and shoreline (Lockley et al., 2006). Shore–parallel trackways have been interpreted as reflecting physical barriers or the preferred route of migration of dinosaurs, but for some examples comprising sets of parallel trackways (Lockley et al., 1986; 2006), a gregarious behaviour has been suggested.

A non-dinosaurian example of shore-parallel tetrapod trackways is the case of mammalian footprints (human and artiodactyl) in a late Holocene beachrock from Rhodes, Greece (Bromley et al., 2009). The inference of palaeoshoreline orientation is further supported by the arrangement of linear forms of *Macaronichnus segregatis* (invertebrate marine trace fossil), perpendicular to the beach slope (Bromley et al., 2009).

A palaeogeographic control on dinosaur trackway orientation has been hypothesized for the carbonate-siliciclastic-lacustrine deposits of the Aptian Enciso Group of the Cameros Basin, Spain (Moratalla and Hernán, 2010). On the basis of a compilation of almost one thousand trackways, Moratalla and Hernán (2010) suggested that the theropod and ornithopod dinosaurs used a preferred regional route across the shallow lacustrine basin, which connected the Ebro and Iberian massifs.

For fluvial floodplain deposits (mostly crevasse splay facies), the orientation of tetrapod trackways is parallel to the mean palaeocurrent direction. In some examples the trackway orientations are bimodal: the Lower Triassic Moenkopi Formation of USA (Peabody, 1947); the Lower Triassic of the Holy Cross Mountains of Poland (Fuglewicz et al., 1990); and the Upper Cretaceous Toreva Formation of USA (Irby and Albright, 2002). Unimodal trackway patterns that parallel the main palaeocurrent direction have been reported from the Albian-Cenomanian of Yukon, Canada (Long et al., 2001) and the Lower Cretaceous Chacarilla Formation of Chile (Rubilar-Rogers et al., 2008). The reason for similar preferential orientation of tetrapod trackways and palaeocurrent indicators in floodplain deposits may be related to a preservational bias or because river channels may offer an easier transit in the river channel belt than the surrounding landscape. A preservational bias is that moist to wet sandy to muddy substrates deposited during episodes of overbank flow are optimal for footprint formation and preservation (Melchor et al., 2012b).

12. Permanent versus intermittent fluvial channel discharge

Most of the trace fossil assemblages in channel facies occur on top or in the upper part of fluvial bars, although ichnofossils can also appear on inactive or abandoned channels, the bottoms of channels, and between deposits of channel bars (Melchor et al., 2012b). Some footprint assemblages of inactive or abandoned channels, interpreted as a channel-related pond formed after abandonment of the active channel (e.g., Lockley et al., 2004; Van Allen et al., 2005), provide no information on the palaeodischarge fluctuations of the fluvial channel. The presence of rhizoliths and mudcracks in the bottom of the main channel is a good indication of ephemeral or intermittent discharge (e.g., Bridge, 2003; Melchor et al., 2012b). Vertebrate footprints occurring at the bottom or within fluvial channel deposits suggest intermittent discharge if they were produced by non-aquatic animals, and permanent discharge if made by aquatic animals.

Examples of vertebrate footprints of non-aquatic animals occurring at the bottom or between channel bars and indicating intermittent discharge include: 1) diverse mammal footprints (assigned to rhinoceros, entelodontids, and camels) described from the base of channel deposits of the Oligocene Brule Formation, USA (Chaffee, 1943), 2) equoid footprints (ichnogenus *Plagiolophustipus*) found at the bottom of meandering-channel deposits of the Oligocene Rocaforte Sandstone, Spain (Astibia et al., 2007), and 3) sauropod dinosaur tracks from the

Maastrichtian North Horn Formation of Utah, USA, occurring on the sole of anastomosed-channel sandstones (Difley and Ekdale, 2002).

Examples of vertebrate track assemblages of non-aquatic animals (including wading birds) that were preserved between channel bars and indicate temporary cessation of channel discharge are: 1) mammalian (*Hipparion*, bovid, and rhinocero) tracks from the gravelly braided fluvial deposits of the Pliocene Osoppo Conglomerate, Italy (Dalla Vecchia and Rustioni, 1996), 2) diverse mammalian (artiodactyl and carnivore) footprints from gravelly braided deposits of the Miocene-Pliocene Ogallala Formation, New Mexico (Williamson and Lucas, 1996), and 3) shorebird tracks in sandy channel deposits of the Neogene Río Negro Formation, Argentina (Melchor, 2009). The latter example displays a moderate density of shorebird tracks (*Gruipeda dominguensis*) on an internal bounding surface of a 3 m thick coset of trough cross-bedded sandstone from a channel-belt deposit (Fig. 9). These tracks indicate temporary ponding of water in the channel and settling of fine-grained sediments (as result of a cessation in river discharge), during the time when the shorebirds were foraging.

Trace fossils of aquatic tetrapods (i.e., crocodiles, aquatic turtles, amphibians) or fish, including swim trace fossils, which appear within or at the bases of fluvial channel deposits indicate permanent fluvial discharge. Ichnoassemblages from the Upper Jurassic Morrison Formation of Colorado and Utah, USA (Foster and Lockley, 1997; Lockley and Foster, 2006) and the Late Cretaceous Tremp Formation of Spain (Vila et al., 2015), involving crocodile swimming traces in channel facies are good examples of this type of interpretations. For example, crocodile tracks (*Hatcherichnus sanjuanensis*) that are associated with tail drag marks and partial imprints occur at the base of a cross-bedded sandstone set within a thick channel deposit of the Morrison Formation (Foster and Lockley, 1997). In this example, the combination of crocodile trace fossils indicate a swimming or basking behaviour, together with the absence of desiccation features, suggest that river discharge was essentially uninterrupted.
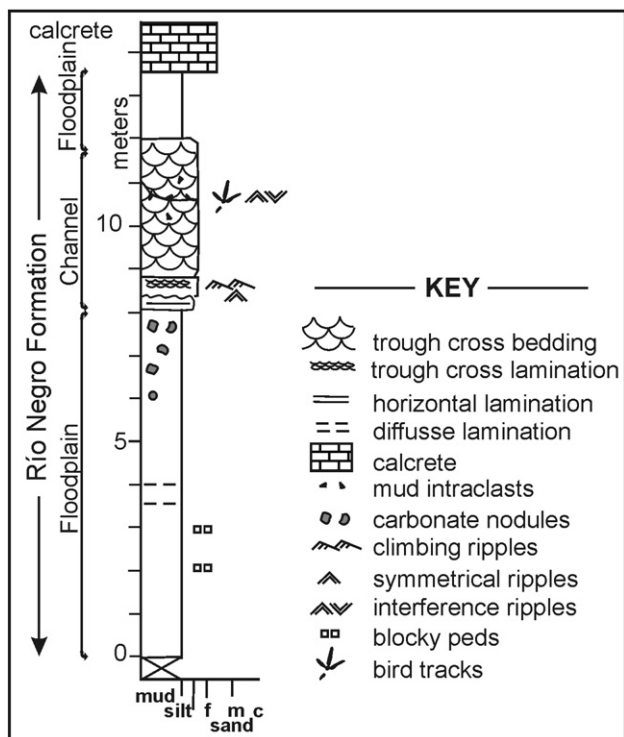

Fig. 9. Sedimentologic log of the Late Miocene to Pliocene Río Negro Formation at La Pampa province, Argentina, showing cross-bedded channel-belt deposits containing shorebird footprints and interference ripples. The bird footprints suggest intermittent channel discharge.

13. Vertebrate ichnofabrics

The study of continental ichnofabrics is in its early stage, and most contributions focus on invertebrate trace fossils. The conceptual and methodological framework for the analysis of invertebrate palaeosol ichnofabrics was proposed by Genise et al. (2004) and Bedatou et al. (2009). Descriptions and interpretations of vertebrate ichnofabrics are rare (see below), although this is not a reflection of their scarcity in the geological record. Studies typically focus on the description and systematics of individual trace fossils as a basis for palaeocommunity reconstruction or ichnofacies analysis. Vertebrate ichnofabric must be analyzed in conjunction with detailed sedimentary facies description to produce a refined palaeoenvironmental interpretation (e.g., McIlroy, 2008; Melchor et al., 2012c).

There has not yet been proposed a conceptual framework or a methodology for the study of vertebrate ichnofabrics. The only exception is the "dinoturbation index" for dinosaurian trampled bedding surfaces by Lockley and Conrad (1989). These authors suggest that the degree of trampling is related to palaeoenvironmental and palaeoecological factors, such as duration of exposure, substrate moisture content, and local population density and frequency of animal activity. A similar measurement is the relative bioturbated area for application to bedding surfaces with two or more footprint ichnotaxa (Krapovickas et al., 2009). This parameter was defined as the percentage of the tracking surface which is bioturbated by each ichnotaxon, and intended as an indication of the activity and the number of individuals (Krapovickas et al., 2009). However, this parameter is strongly influenced by the size of the trackmaker and of dubious utility. Both parameters are intended for application in bedding planes.

One of the most commonly described vertebrate ichnofabrics involves heavily bioturbated beds trampled by vertebrates, whit few or no discrete trace fossils (e.g., Laporte and Behrensmeyer, 1980; Ashley and Liutkus, 2002; Jennings et al., 2006; Scott et al., 2012b). There are also a few descriptions of vertebrate ichnofabrics with discrete trace fossils (e.g., Fornós et al., 2002; Tobin, 2004; Melchor et al., 2012c).

13.1. Massive beds due to trampling by vertebrates

Massive siltstone and sandstone beds may be due to intense trampling by vertebrates, especially on lake margins, lacustrine deltas, spring-fed wetlands, and emergent fluvial bars (Laporte and Behrensmeyer, 1980; Ashley and Liutkus, 2002; Scott et al., 2012b). In order to produce massive beds along lake margins, it is necessary that either wave or current processes be reduced or that vertebrate trampling intensity overcomes the potential physical reworking by waves or currents. Pliocene-Pleistocene examples of heavily bioturbated beds due to trampling by vertebrates from northern Kenya, were recognized as massive beds with unoriented mica flakes and bits and pieces of bone with the long axes at high angles to bedding (Laporte and Behrensmeyer, 1980). Bone remains in these beds are usually broken and splintered, suggesting breakage by vertebrate trampling (Laporte and Behrensmeyer, 1980). The upper part of the massive beds may preserve scattered footprints in cross-section, whereas their bases can exhibit local depressions that may be interpreted as game trails (Laporte and Behrensmeyer, 1980). Jennings et al. (2006) described an Upper Jurassic example of carbonate lacustrine mudflats trampled by dinosaurs that also contains abundant broken bones and may have been produced by a similar process.

Massive, Pleistocene-Holocene delta plain to delta front silt deposits of Lake Bogoria, Kenya, exhibit an ichnofabric of bubble pores and ped-like mud clumps interpreted as results of flamingo trampling of wet mud (Scott et al., 2012b). Bubble pores are large (up to 1 cm), irregular and commonly pinched at one end, which make them distinguishable from the ovoid and smaller voids of the sponge pore

fabric (Noffke et al., 2001) related to microbial mats, and birdseye structure (e.g., Shinn, 1968), occurring in carbonate rocks.

Massive silty clay and claystone beds due to intense bioturbation by large vertebrates has been recognized in modern wetlands of the Ngorongoro Crater and in Pliocene-Pleistocene sediments of Olduvai Gorge, Tanzania (Ashley and Liutkus, 2002; Deocampo, 2002; Liutkus and Ashley, 2003). Massive silty claystones in these examples are 0.15 to >1.00 m thick and contain bone fragments, occasional carbonate rhizoliths, and silicified plant remains (Ashley and Liutkus, 2002). Footprints are discernible at the tops of these beds and can be traced laterally to trackways. Distinctive U-shaped depressions about 1.5 m wide and 1 m deep infilled by massive silty claystone may be recognized in the bottom of these massive deposits. They are interpreted as hippopotamus trails in a soupy substrate (Ashley and Liutkus, 2002; Deocampo, 2002).

13.2. Vertebrate ichnofabrics with discrete trace fossils

The published examples of vertebrate ichnofabrics with discrete ichnofossils include a Pleistocene palaeosol in loess from Nebraska, USA, Pleistocene carbonate aeolian dunes from Mallorca, Spain, and late Miocene and Holocene siliciclastic interdune deposits from Patagonia, Argentina.

The example of a vertebrate burrow ichnofabric from a palaeosol is from the late Wisconsinan loess deposits of the Gilman Canyon Formation of Nebraska, USA (Tobin, 2004). The ichnofabric is composed of burrow systems of four rodent genera (*Spermophilus*, *Cynomys*, *Thomomys*, and *Geomys*) and probable Mustelidae predation holes on the rodent burrows, which were distinguished by their tunnel diameter, depth to the top of the palaeosol and architectural style (Tobin, 2004). This ichnofabric accounts for up to 10% of outcrop exposures and is uniformly developed in a maximum stratigraphic thickness of 4 m. The presence of a uniform bioturbation intensity as opposed to a downward decline expected if the rodents burrowed from a single surface, suggest that the development of the ichnofabric was continuous through the slow deposition of the Gilman Canyon Formation (Tobin, 2004). In consequence, this type of vertebrate burrow ichnofabric can be indicative of a cumulative soil profile.

Pleistocene goat trampling of carbonate aeoliansands from Mallorca (Balearic Islands) produced a very distinctive ichnofabric (Fornós et al., 2002). The tracks, attributed to the extinct caprine *Myotragus balearicus*, are found in cliff-front dunes and sand ramp deposits formed during a sea level lowstand of the last glacial period (Fornós et al., 2002). In sections perpendicular to bedding, the ichnofabric appears as several concave upward laminae containing multiple and concentrically stacked sediment packages bounded by shear planes ("pressure pads"; after Fornós et al., 2002). Deeply penetrating footprints and associated deformation structures suggest production in moist dune sand, probably

during wet winters, and associated undisturbed foreset laminae were linked to dry summers. In consequence, the presence of this ichnofabric alternating with undisturbed laminae would reflects a seasonal climate (Fornós et al., 2002).

Late Miocene and Holocene interdune deposits of Argentina contain large meniscate burrows, *Nagtuichnus meuleni*, that were probably produced by pink fairy armadillos (*Chlamyphorus truncatus*, Dasypodidae) (Melchor et al., 2012c). This ichnotaxon may comprise highly bioturbated ichnofabrics (Fig. 10), with up to 60% of the surface area disturbed by burrowing by vertebrates. Associated invertebrate ichnofossils are *Skolithos linearis* and thin root traces. *Nagtuichnus meuleni* and the resultant ichnofabric seem to be restricted to, and indicative of, sandy dry to damp interdune facies (Melchor et al., 2012c), although more examples are necessary to confirm this inference.

14. Use of vertebrate ichnofacies in palaeoenvironmental analysis

There is still much debate and disagreement on the nature of each vertebrate ichnofacies, the criteria used in their definition and even the usefulness of the concept in vertebrate ichnology. The criteria used for the recognition of vertebrate ichnofacies are not the same as those applied to invertebrate ichnofacies. Continental invertebrate ichnofacies are thought to be controlled by the position of the water table and/or climate and plant formation, whereas the factors controlling the distribution of vertebrate trace fossils are poorly known (Buatois and Mángano, 2011). Martin G. Lockley and others (Lockley et al., 1994; Lockley, 2007) recognized a number of candidates for vertebrate ichnofacies, emphasizing the recurrence of certain types of tetrapod footprints in definite sedimentary facies and (palaeo)environments, and highlighting their potential use in palaeocology and biostratigraphy. Most of these potential ichnofacies are better considered as ichnocoenoses (Hunt and Lucas, 2007), because they represent biological communities with restricted temporal and geographical ranges (Melchor et al., 2006; 2012b). Hunt and Lucas (2007) built on the proposal by Lockley et al. (1994), and presented a number of newly defined vertebrate ichnofacies that are composed of individual ichnocoenoses. The vertebrate ichnofacies of Hunt and Lucas (2007) were intended to be parallel to invertebrate archetypal ichnofacies, although some of them (for example, *Batrachichnus* and *Brontopodus* ichnofacies) are not distinguished by objective morphological criteria and/or display limited temporal range. In spite of these caveats, the proposal by Hunt and Lucas (2007) is herein considered a general template for further discussion and refinement. In the next paragraphs, the palaeoenvironmental meaning of vertebrate ichnofacies proposed by Hunt and Lucas (2007) and other potential vertebrate ichnofacies will be discussed. As noted below, the recognition of most vertebrate ichnofacies, as currently defined, adds little palaeoenvironmental information to the sedimentary facies analysis.
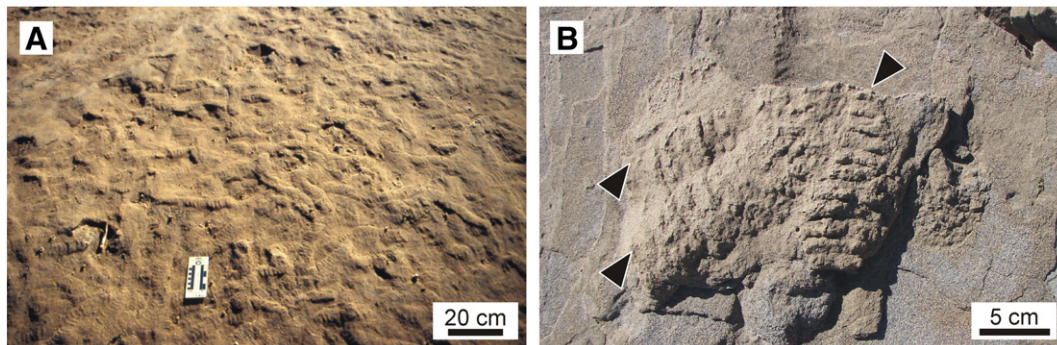

Fig. 10. Examples of the *Nagtuichnus* ichnofabric from dry to damp interdune deposits. (A) Plan view of Holocene deposits of the Gran Salitral, La Pampa province, Argentina. Modified from Melchor et al. (2012c). (B) View parallel to bedding from the Late Miocene-Pliocene Río Negro Formation near Carmen de Patagones, Buenos Aires province, Argentina. Four cross-cutting *Nagtuichnus* specimens are arrowed.

14.1. Archetypal vertebrate ichnofacies

Hunt and Lucas (2007) recognized five archetypal ichnofacies: *Chelichnus*, *Batrachichnus*, *Brontopodus*, *Grallator* and *Characichnos*. The *Chelichnus* ichnofacies is represented by low diversity assemblages of tetrapod footprints of equant shape (i.e., similar length and width), short digit imprints and manus and pes of similar size, indicative of aeolian dune deposits. This ichnofacies can be broadened to incorporate the invertebrate ichnofossils of sandy aeolian successions –the *Chelichnus-Octopodichnus* ichnofacies (Lockley, 2007). Also proposed for aeolian dune deposits, the invertebrate *Entradichnus* ichnofacies (Ekdale et al., 2007), includes vertebrate footprints as an accessory component.

The *Batrachichnus* ichnofacies was proposed to include medium to high diversity assemblages of quadrupedal carnivores. As defined by Hunt and Lucas (2007), this ichnofacies have a very broad environmental meaning, as it was recorded from tidal flat to fluvial plain settings.

The Late Jurassic to Late Cretaceous *Brontopodus* ichnofacies of Hunt and Lucas (2007), was proposed to characterize moderately diverse ichnofaunas with a majority of tracks of terrestrial, quadrupedal herbivores. This ichnofacies also has a very broad environmental meaning, resulting from those of the component ichnocoenoses (or subichnofacies), which are more restricted environmentally (Lockley et al., 1994; Hunt and Lucas, 2007): ceratopsian and ornithopod footprint assemblages are typical of coastal plains; the ornithopod *Caririchnium* ichnocoenosis is found in clastic marine shorelines; and the *Brontopodus* and *Emydhipus* ichnocoenoses are found in carbonate marine shorelines. A recent revision of the occurrences of body fossils and trackways of sauropod dinosaurs reveals a preferred environmental distribution of non-titanosaur and titanosaur sauropods (Mannion and Upchurch, 2010). Non-titanosaur sauropods (including ichnogenus *Parabrontopodus*, reflecting narrow-gauge trackways) apparently preferred coastal environments such as carbonate platforms, whereas titanosaurs (including the ichnogenus *Brontopodus*, reflecting wide-gauge trackways) preferred inland environments such as fluvio-lacustrine systems (Lockley et al., 1994; Mannion and Upchurch, 2010).

The *Grallator* ichnofacies of Hunt and Lucas (2007) is typified by trace fossil assemblages dominated by bipedal tridactyl or tetradactyl tracks of avian and non-avian theropods. This ichnofacies is a generalization of the well-defined "shorebird ichnofacies" of Lockley et al. (1994), which was erected to highlight the association of avian footprints with lacustrine margin deposits, including floodplain ponds. However, some examples of bird footprint-dominated trace fossil assemblages are also known from lagoonal (e.g., Doyle et al., 2000) and tidal flat settings (e.g., Payros et al., 2000).

The *Characichnos* ichnofacies was proposed to refer to assemblages that contain a majority of vertebrate swim trace fossils, mostly groups of parallel scratch traces (ichnogenus *Characichnos*) and sinusoidal trails of fish origin (ichnogenus *Undichna*) from lacustrine shorelines (Hunt and Lucas, 2007). This ichnofacies displays a considerable overlap with the invertebrate *Mermia* ichnofacies, typical of lacustrine deposits, because both share sinusoidal trails (*Undichna*). The identification of the *Characichnos* ichnofacies suggests continental or marine water-lain substrates that were never exposed to air. The *Chelonipus* ichnocoenosis (Lockley and Foster, 2006) was proposed to distinguish Late Triassic to Cretaceous turtle swim-traces in fluvial-channel deposits and can be considered under the *Characichnos* ichnofacies. The *Chelonipus* ichnocoenosis may be indicative of permanent subaqueous substrates deposited in fluvial channels.

14.2. Potential vertebrate ichnofacies

Other potential ichnoassemblages that may constitute ichnofacies but that are poorly known are the incipient vertebrate burrow ichnofacies and two coprolite ichnofacies or coprofacies. The incipient tetrapod burrow ichnofacies (Melchor et al., 2012b) is represented by the occurrence of large vertebrate burrows related to palaeosols, with examples from the Permian to Recent. The vertebrate burrows may exhibit a varied morphology, including a helical pattern with a terminal chamber (ichnogenus *Daimonelix*) or a low-angle ramp tunnel with a rounded end (that may or may not be enlarged). Associated trace fossils are rhizoliths, meniscate burrows, and rare insect trace fossils. These examples commonly appear in well-drained soils with carbonate nodules or nodular horizons developed under arid or semiarid climate (e.g., Martin and Bennett, 1977; Smith, 1987; Groenewald et al., 2001; Gobetz and Martin, 2006; Colombi et al., 2008; Sidor et al., 2008; Colombi et al., 2012). The presence of vertebrate burrows, especially if occurring in moderate to high density with abundant associated rhizoliths, is indicative of the topmost horizons of soils and well-drained soil profiles (Retallack, 1990; Gobetz, 2006). For example, in the case of the vertical helical burrow *Daimonelix*, its maximum vertical length has been considered as a minimum depth to the water table (Toots, 1963; Martin and Bennett, 1977; Meyer, 1999). A seasonal climate is inferred for Miocene rodent nut caches related to an interdune palaeosol from Germany (Gee et al., 2003) and also for early Miocene helical burrows (*Daimonelix*) from USA (Meyer, 1999). To summarize, the proposed incipient tetrapod burrow ichnofacies reflects well-drained calcareous soil profiles developed under arid or semi-arid climate. There are some examples of vertebrate burrows from aeolian sequences that are not clearly linked to palaeosols (Loope, 2006a; Loope, 2008; Melchor et al., 2012c), in consequence they do not fit in the proposed vertebrate burrow ichnofacies.

Two coprolite ichnofacies have been proposed: *Heteropolacopros* and *Dicynodontocopros* (Hunt et al., 2007). The *Heteropolacopros* ichnofacies is characterized by the presence of microspiral heteropolar coprolites, assigned to xenacanth sharks or lungfish, which occur in Permian-Triassic fluvial redbeds, although a more restricted facies discrimination is not possible at present. Large herbivore (dicynodont?) coprolites from swampy environments are the typical components of the *Dicynodontocopros* ichnofacies (Hunt et al., 2007).

15. Concluding remarks

This paper highlights the contributions of vertebrate trace fossils in the analysis of sedimentary environments and the topics that are poorly known and may become the focus of future research. Although vertebrate trace fossils are essentially sedimentary structures of biogenic origin, they are not always described in an adequate sedimentological framework (sedimentary facies and interpreted environments). Instead, vertebrate trace fossils are sometimes described and interpreted with no reference to hosting sedimentary facies. This practice will result in a study that, although acceptable as an original and significant contribution to science, precludes any sedimentological application of the described trace fossils. It is suggested that, the regular incorporation of a solid sedimentary facies scheme in the description of individual vertebrate trace fossils assemblages or ichnofabrics, will be highly beneficial for the development of new vertebrate ichnological tools and concepts of application to palaeoenvironmental analysis.

One theme that needs to be explored further is footprint formation, and its dependence on different substrate types (including the poorly known pyroclastic materials), their shear strength, role of algal mats, and the response of substrates to indentation by animals of different size and foot shapes. Although significant improvements have been made in the last decades, footprint formation and preservation is poorly understood and we need more experiments and field observations in modern settings. Similarly, the zonation of lacustrine margins on the basis of avian footprints in alkaline/saline basins (Cohen et al., 1991; Alonso, 2012; Scott et al., 2012b) and its potential application to exploration in evaporite sequences needs to be tested in fossil examples.

It is also necessary to develop a conceptual framework and a workable methodology for the description and interpretation of vertebrate ichnofabrics, as they can add significant palaeoenvironmental

information that cannot be obtained from sedimentary facies alone. The case of the *Nagtuichnus* ichnofabrics, which seem to indicate dry to damp interdune facies (Melchor et al., 2012c), is a good example that ichnofabric studies, aided by neoichnological observations or experiments, can yield new valuable tools for enhanced interpretation of sedimentary sequences.

The vertebrate ichnofacies model is still debated and further refinements are needed in order for it to be accepted and used by the ichnological community. At its present state, the recognition of any of the archetypal vertebrate ichnofacies adds little information in terms of diagnostic or accessory features for the interpretation of the sedimentary environment. The only notable exceptions are probably the "shorebird ichnofacies" of lakeshore facies and the *Chelichnus* ichnofacies of aeolian dune cross-strata. The potential vertebrate burrow ichnofacies is too broadly defined at its present state, but may be susceptible to refinement in the near future.

Acknowledgments

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